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Conspecific cues mediate habitat selection and reproductive performance in a haplodiploid spider mite

Nuwan Weerawansha[a,b,*], Qiao Wang[a], and Xiong Zhao He[a,*]

[a]School of Agriculture and Environment, Massey University, Private Bag 11222, Palmerston North, 4472, New Zealand
[b]Faculty of Animal Science and Export Agriculture, Uva Wellassa University of Sri Lanka, Passara Road, Badulla 90000, Sri Lanka
*Address correspondence to Nuwan Weerawansha. E-mail: nuwanw@uwu.ac.lk; Xiong Z. He. E-mail: x.z.he@massey.ac.nz
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Abstract

Selection of a suitable habitat by animals before settlement is critical for their survival and reproduction. In silk-spinning arthropods like spider mites, denser webs offer protection from predation and serve as a dispersal mode. Settling in habitats with the presence of conspecifics and silk webs can benefit the habitat-searching females. Silk and conspecifics usually coexist, but their distinct effects on female colonization have received little attention. In this study, we used a haplodiploid spider mite, *Tetranychus ludeni* Zacher (Acari: Tetranychidae), to examine the impact of conspecific cues, including cues from ovipositing conspecifics and silk, on habitat selection and subsequent reproductive performance of females. Results show that females significantly preferred habitats with cues from neighboring conspecifics and silk and neighboring conspecifics induced additive effect to that of silk on habitat selection. Conspecific cues did not boost female reproduction but facilitated females laying larger eggs that were more likely to be fertilized and to develop into daughters. When given a choice between silk-covered and clean habitats, females preferred silk-covered habitats, laid a similar number of eggs with similar size, but produced more daughters, suggesting that *T. ludeni* females can adjust the size threshold for fertilization in response to the current social environment. Knowledge of this study improves our understanding of spider mite habitat selection and post-settlement reproductive performance behaviors.

Key words: conspecific cues, habitat selection, reproduction, sex allocation.

Habitat selection, the phenomenon by which individuals decide to use or settle in a given site, is certainly important for growth, survival, and reproduction (Vollrath 1987; Reed and Dobson 1993; Vinson 1998; Schuck-Paim and Alonso 2001; Fletcher and Miller 2008; Clotuche et al. 2013a). Habitat selection by animals is not random. Much evidence suggests that animals select habitats by using information such as tactile, visual, acoustic, or chemical cues to explicitly assess habitat quality (Godfray 1994; Schmidt et al. 2010; Aquino et al. 2012; Buxton et al. 2020; Bowen-MacLean et al. 2021). It is frequently reported that social species may use multiple conspecific cues for breeding-site selection (Reed and Dobson 1993), because settling near conspecifics brings various benefits including reduced searching costs (Fletcher 2006) and incidental assessment of habitat quality (Doligez et al. 2003), and increasing fitness gains through the Allee effect (i.e., positive correlation between population density and fitness of individuals) (Courchamp et al. 2008; Astudillo Fernandez et al. 2012a, 2012b).

In silk-spinning arthropods, silken threads are indicative of the presence of conspecifics and thus can be used as a social cue for group cohesion or for selection of a place to live (Saffre et al. 1999; Schuck-Paim and Alonso 2001; Bernard and Krafft 2002; Despland and Le Huu 2007; Yano 2012; Clotuche et al. 2014). Spider mites from genus *Tetranychus* produce silk webs while walking (Saito 1977; Clotuche et al. 2012a). The dense webs may protect mites from predation (McMurtry

et al. 1970; Sabelis 1985; Tien et al. 2009; Dittmann and Schausberger 2017), bad weather conditions (Davis 1952; Linke 1953) and pesticides (McMurtry et al. 1970) and serve as modes of dispersal (Saito 1977; Gerson 1985; Yano 2008; Clotuche et al. 2013b). Additionally, silk may act as the substrate for sex pheromones (McGregor 1950; Saito 1977, 1979; Sabelis 1985; Sabelis and Bakker 1992; Zhang et al. 2002; Yano 2008; Clotuche et al. 2009, 2011, 2012b, 2014; Tien et al. 2009; Le Goff 2011). Moreover, as spinning silk is costly due to energy and protein expenditure (Hazan et al. 1974), mothers living on leaves over which silk is already present may minimize their silk production and allocate more resources to reproduction (Oku et al. 2009; Le Goff et al. 2010) and survival (Le Goff et al. 2010; Yano 2012). Considering the given benefits, spider mites usually tend to settle in the presence of conspecifics and their silk directly by perceiving visual and olfactory cues emitted by ovipositing conspecifics and/or indirectly by tracking olfactory cues from feces and silk (Royalty et al. 1993; Clotuche 2011; Le Goff 2011; Bowen-MacLean et al. 2021; Schausberger et al. 2021). Nevertheless, in nature, conspecifics and silk usually exist concurrently; whether they have distinct effects on settlement and reproduction of colonizers has received little attention. Furthermore, the behavioral responses of spider mites are usually stronger in the presence of multiple cues than that of an individual cue alone (Azandémè-Hounmalon et al. 2016).

Spider mites usually colonize and feed on the underside of leaves of host plants by piercing cells and extracting cell contents (Dhooria 2016), leading to scramble competition for food resources (Krips et al. 1998). Aggregating in a habitat may induce overcrowding conditions which will accelerate food depletion in the natal environment (Krips et al. 1998; Clotuche et al. 2011; Bitume et al. 2013). Therefore, females must develop strategies to minimize resource competition with conspecifics and their offspring. *Tetranychus* spp. are haplodiploid species, mated females raise haploid sons from unfertilized eggs and diploid daughters through fertilized eggs (Young et al. 1986; Macke et al. 2011; Zhou et al. 2018). They are capable of manipulating offspring sex ratio by adjusting egg size and fertilizing larger eggs that develop into daughters (Macke et al. 2011, 2012; Weerawansha et al. 2022), or through sex allocation distortion by *Wolbachia* bacteria, which is driven by increasing egg size, hereby promoting egg fertilization (Wybouw et al. 2023). In spider mites, females usually mate at emergence and then disperse from the dense environments (Brandenburg and Kennedy 1982; Boykin and Campbell 1984; Margolies and Kennedy 1985; Li and Margolies 1993; Yano 2004; Osakabe et al. 2008; Clotuche et al. 2013c). *Tetranychus* species have a high female-biased sex ratio, which will reduce the intensity of local mate competition and local resource competition (Macke et al. 2012; Weerawansha et al. 2023). Yet, it remains unclear whether and how females adjust offspring sex ratio in response to socio-environmental cues in their surroundings.

Here, we used the spider mite, *Tetranychus ludeni* Zacher, as a model species to examine whether the settlement and reproductive performance of mated females were influenced by the presence of conspecific cues. Based on the knowledge outlined above, we tested two hypotheses that 1) females are more likely to settle, lay more eggs, and produce a higher female-biased offspring sex ratio in habitats covered with conspecific silk compared with the clean ones (i.e., no silk and no conspecifics), and 2) females tend to settle, lay more eggs, and produce a higher female-biased offspring sex ratio on silk-covered habitats with conspecifics occupying the neighboring habitats, compared with the silk-covered or clean habitats. The results of this study are anticipated to enhance our understanding of the mechanisms of habitat selection and the post-settlement reproductive performance of silk-spinning arthropods.

Materials and Methods

Mite colony and experimental conditions

We started a colony of *T. ludeni* by collecting adults on *Passiflora mollissima* Kunth (Malpighiales: Passifloraceae) in Palmerston North, New Zealand, and reared them on common bean plants *Phaseolus vulgaris* L. (Fabales: Fabaceae) grown in pots. We used the first expanded leaves of 1- to 2-week-old plants for the experiment. The colony was maintained, and experiments were conducted under environmental conditions of 25 ± 1 °C, 40 ± 10% RH, and 16:8 h (light:dark) photoperiod.

### Preparation of mites for experiments

To obtain mated females for the experiment, we haphazardly collected 50 female deutonymphs from the colony and introduced them onto a bean leaf square (2 cm × 2 cm) placed on a water-saturated cotton pad in a Petri dish (9.5 cm diameter × 1.0 cm height) with a mesh-covered ventilation hole (1.0 cm diameter) in the lid. Deutonymphs were allowed to develop to the quiescent stage. We then introduced 15 newly emerged male adults produced by virgin females onto the leaf square. We maintained these mites for 24 h to allow mating to occur on female emergence. The mated females were then employed for the experiment. Sixty such Petri dishes were prepared for the experiment. We obtained about 2,500 mated female adults from those dishes.

Experimental procedures

To test the effects of the presence of conspecific cues on mated female dispersal and reproduction, we set up 3 habitat selection treatments: (1) Silk vs. NoCue, females were offered a choice of 2 habitats, 1 with silk (Silk) and another with no cue (NoCue) (Figure 1A); (2) Silk+Consps vs. NoCue, females were offered a choice of 2 habitats, 1 with silk and 5 neighboring conspecifics (Silk + Consps) and another with no cue (NoCue) (Figure 1B), and (3) Silk+Consps vs. Silk, females were offered a choice of 2 habitats, 1 with silk and 5 neighboring conspecifics (Silk+Consps) and another with silk (Silk) (Figure 1C). There were 20 replicates for each treatment. The experimental females and neighboring conspecifics were prepared as mentioned above, and they were haphazardly selected with the same age (i.e., 1 day old) when used for the experiment.

To obtain a "silk-covered" section, we introduced 15 mated females prepared as mentioned above onto a leaf square (4 cm × 4.6 cm) placed upside down on a water-saturated cotton pad in an above Petri dish, and allowed them to deposit silk for 24 h (Figure 1, top dish), after which time we removed the females, eggs, and feces using a fine brush. The "silk-covered" leaf square was then split into 2 equal sections (4 cm × 2.2 cm) by cutting off a 2-mm-wide leaf strip using a knife along its mid-plane, so that the water-saturated cotton pad could support the parafilm square (1 cm × 1 cm) from which the test females selected and dispersed to either habitat (Figure 1A–C). To ensure a clean leaf surface devoid of conspecific cues from silk and feces (Figure 1A,B), we meticulously washed 1 of the 2 leaf sections with distilled water and a fine hairbrush, and then left the washed section to air-dry for 1 h in the laboratory. These processes aimed to minimize the difference in leaf quality between the "silk-covered" and clean leaf sections due to mite feeding. Each leaf section was further divided into 2 equal sub-sections (4 cm × 1 cm) (Figure 1A,B). This division was achieved by cutting off a 2-mm-wide leaf strip from one-fourth the length of one side of the original leaf square (Figure 1A–C). Depending on the treatment, we introduced 5 mated females onto the far neighboring leaf sub-section creating the habitat condition of presence of conspecifics (Figure 1B and C). We placed a parafilm square in the center that bridged the 2 neighboring leaf sub-sections (Figure 1A–C). We then introduced 15 mated females onto the parafilm square and allowed them to disperse and settle on the 2 inner neighboring leaf sub-sections (Figure 1A–C) without any physical contact with the neighboring conspecifics (Figure 1B and C). After 24 h, we counted and recorded the number of dispersed individuals that finally settled on each of neighboring leaf sub-sections. For each replicate, we calculated the overall dispersal rate (i.e., proportion of females dispersed) as the number of dispersed females/total number of test females (i.e., *n* = 15), and habitat selection (i.e., proportion of dispersed females settling
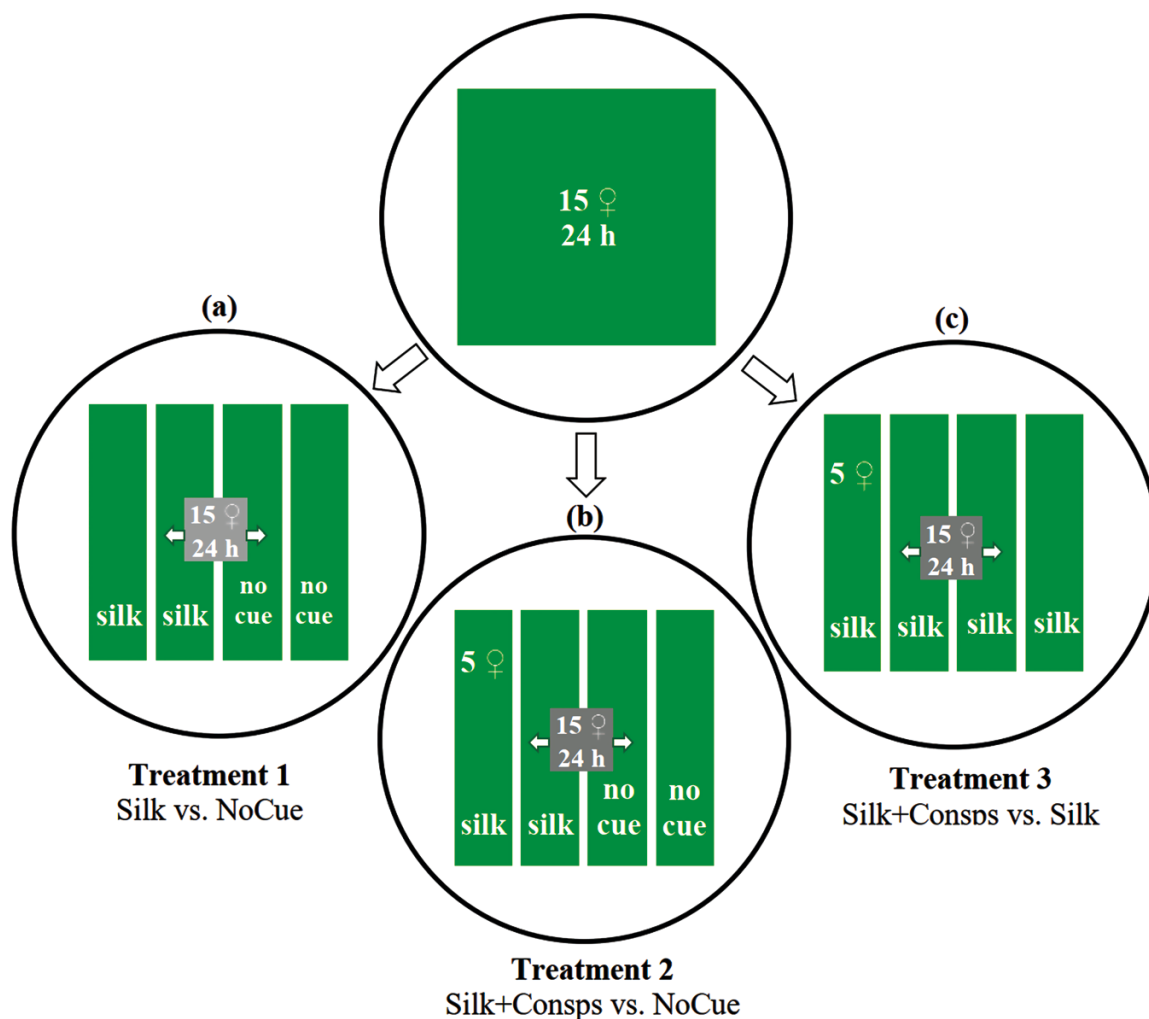
Figure 1. Diagram of experimental design to test the effects of presence of conspecific cues on habitat selection and reproduction of *Tetranychus ludeni* females. The test females were able to detect cues from the far leaf sub-sections but unable to settle on these sub-sections.

on a habitat) as the number of females settling on a selected habitat/total number of dispersed females. To eliminate the variance between treatments caused by individual mites from different batches, 3–5 replications of each treatment were daily performed simultaneously.

To test whether the selected habitat environment affecting the subsequent reproductive fitness of mated females, we removed parafilm bridges after counting the number of dispersers and separated the cotton pad in the Petri dish into 2 equal halves by cutting along its mid-vertical line using scissors while keeping the leaf sections (i.e., one inner and one outer sub-sections) intact. We then transferred each half of the cotton pad along with the dispersed mites and its adjacent leaf sub-section containing 5 conspecifics, no cue or silk onto a new Petri dish. We allowed the females to oviposit in situ for 5 days. We checked each Petri dish twice a day. The total number of eggs laid in a selected habitat was counted. Due to the different number of females settled on different selected habitats, we also calculated the number of eggs laid by a female on a habitat (i.e., total number of eggs laid on a selected habitat/number of females settling on that habitat). As egg size does not change before hatching (usually in 3 days under the experimental conditions), we haphazardly selected all or a maximum of 20 eggs from each test leaf section on

the 3rd day of oviposition and measured the egg diameter under a stereomicroscope (Leica MZ12, Germany) connected to a digital camera (Olympus SC30, Japan) and an imaging software (CellSens® GS-ST-V1.7, Olympus, Japan). We then calculated the egg size (volume $=4/3\pi r^3$), where r is the radius (= diameter/2). The larvae hatching from the eggs were allowed to feed in situ; after developing into protonymphs they were transferred onto a clean leaf square (2 cm × 2 cm), where they developed into adults. Newly emerged adults were sexed and removed from the leaf square daily. We calculated the offspring sex ratio (i.e., proportion of daughters) as the number of daughters/total number of offspring, and immature survival rate as the number of eggs laid/total number of offspring.

Statistical analysis

We analyzed all data using SAS 9.4 (SAS Institute Inc., Cary, NC). Data on the percentage of mated females dispersing from the parafilm square to any habitat in the 3 experimental settings (treatments) (Figure 2A) were analyzed using a generalized linear model with a *Logit* function and a binomial distribution (GLIMMIX procedure). Their differences were multiply compared using an adjusted-Tukey test. Data on habitat selection (Figure 2B), number
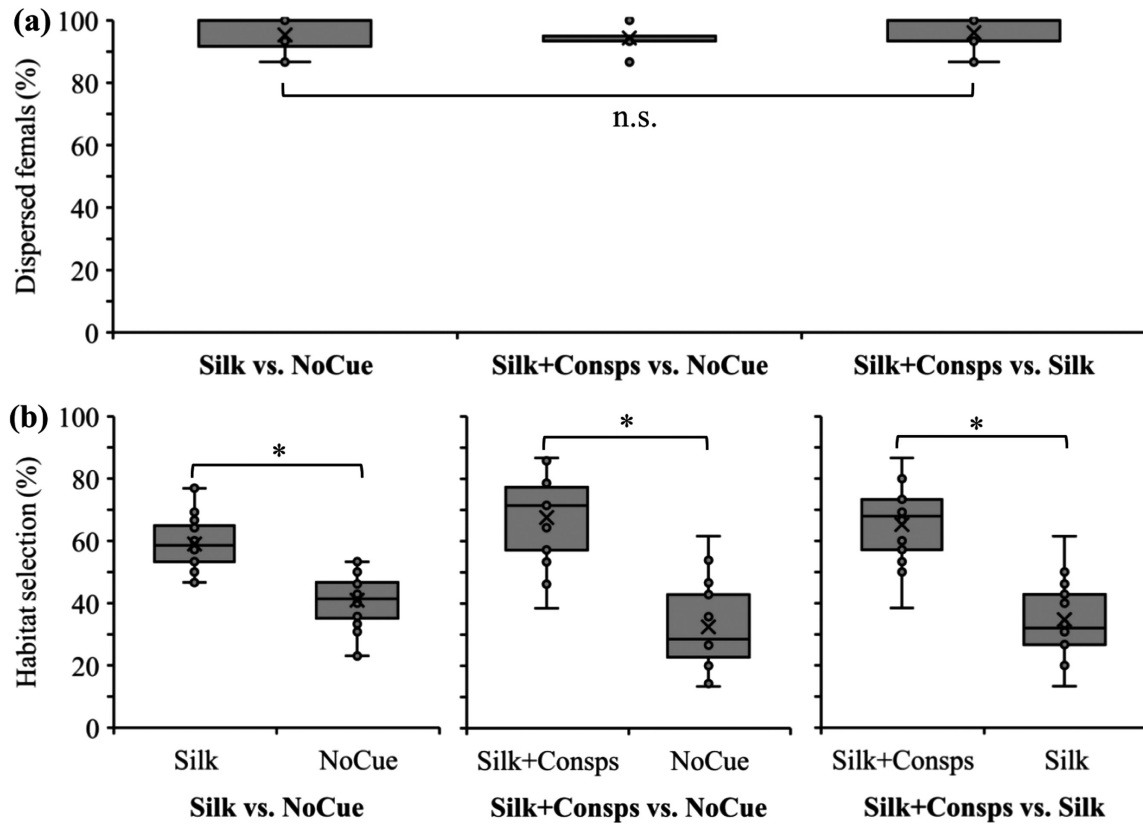
Figure 2. Effects of presence of conspecific cues on female dispersal (A) and habitat selection (B) in *Tetranychus ludeni*. n.s. indicates non-significant difference ($P > 0.05$), and * indicates significant difference ($P < 0.05$).

of eggs laid per female, total number of eggs laid in a selected habitat, egg size, offspring sex ratio (proportion of daughters) (Figure 3), and immature survival rate (Figure 4) were normally distributed (Shapiro–Wilk test, univariate procedure). As these parameters were paired datasets within each replicate of a given treatment, the difference between the 2 selected habitats was compared using a paired-*t* test (TTEST procedure).

Results

Dispersal and settlement

Among the test individuals, the percentage of mites dispersing from the parafilm square was not significantly different between the three experimental settings ($F_{2,57} = 0.45$, $P = 0.6384$) (Figure 2A). However, among the dispersers, significantly more females selected and settled in habitats with the presence of neighboring conspecifics and/or silk, i.e., they preferred Silk to NoCue habitat in treatment Silk vs. NoCue ($t_{19} = 4.45$, $P = 0.0003$), preferred Silk + Consps to NoCue habitat in treatment Silk + Consps vs. NoCue ($t_{19} = 5.97$, $P < 0.0001$), and preferred Silk + Consps to Silk habitat in treatment Silk + Consps vs. Silk ($t_{19} = 5.70$, $P < 0.0001$) (Figure 2B).

Reproduction

The number of eggs laid by a female after settling in a selected habitat was not significantly influenced by the presence of conspecific cues ($t_{19} = -0.98$, $P = 0.3379$ for Silk vs. NoCue; $t_{19} = -0.47$, $P = 0.6424$ for Silk + Consps vs. NoCue; $t_{19} = -1.94$, $P = 0.0676$ for Silk + Consps vs. Silk) (Figure

3A). However, due to significantly more females settling in habitats with the presence of conspecific cues (Figure 2B), the total number of eggs laid in the preferred habitats was significantly higher, i.e., Silk > NoCue in treatment Silk vs. NoCue ($t_{19} = 5.13$, $P < 0.0001$), Silk + Consps > NoCue in treatment Silk + Consps vs. NoCue ($t_{19} = 6.75$, $P < 0.0001$), and Silk + Consps > Silk in treatment Silk + Consps vs. Silk ($t_{19} = 6.48$, $P < 0.0001$) (Figure 3B).

Silk cue alone had no significant effect on egg size compared with NoCue ($t_{19} = 0.83$, $P = 0.4169$) (Figure 3C); however, eggs laid by females in habitats with multiple conspecific cues were significantly larger than that with no cue ($t_{19} = 4.83$, $P < 0.0001$) or with silk cue only ($t_{19} = 5.29$, $P < 0.0001$) (Figure 3C). The proportion of daughters was significantly higher in habitats with the presence of conspecifics and/or silk cue, i.e., Silk > NoCue in treatment Silk vs. NoCue ($t_{19} = 5.06$, $P < 0.0001$), Silk + Consps > NoCue in treatment Silk + Consps vs. NoCue ($t_{19} = 10.00$, $P < 0.0001$), and Silk + Consps > Silk in treatment Silk + Consps vs. Silk ($t_{19} = 6.04$, $P < 0.0001$) (Figure 3D).

Conspecific cues had no significant effect on the immature survival ($t_{19} = -1.98$, $P = 0.0629$ for Silk vs. NoCue; $t_{19} = 1.12$, $P = 0.2779$ for Silk + Consps vs. NoCue; $t_{19} = 0.19$, $P = 0.8506$ for Silk + Consps vs. Silk) (Figure 4).

Discussion

In the present study, we differentiated the effects of silk and neighboring conspecifics on habitat selection in spider mite females. We demonstrate that although *T. ludeni* females had similar possibility to disperse regardless of experimental
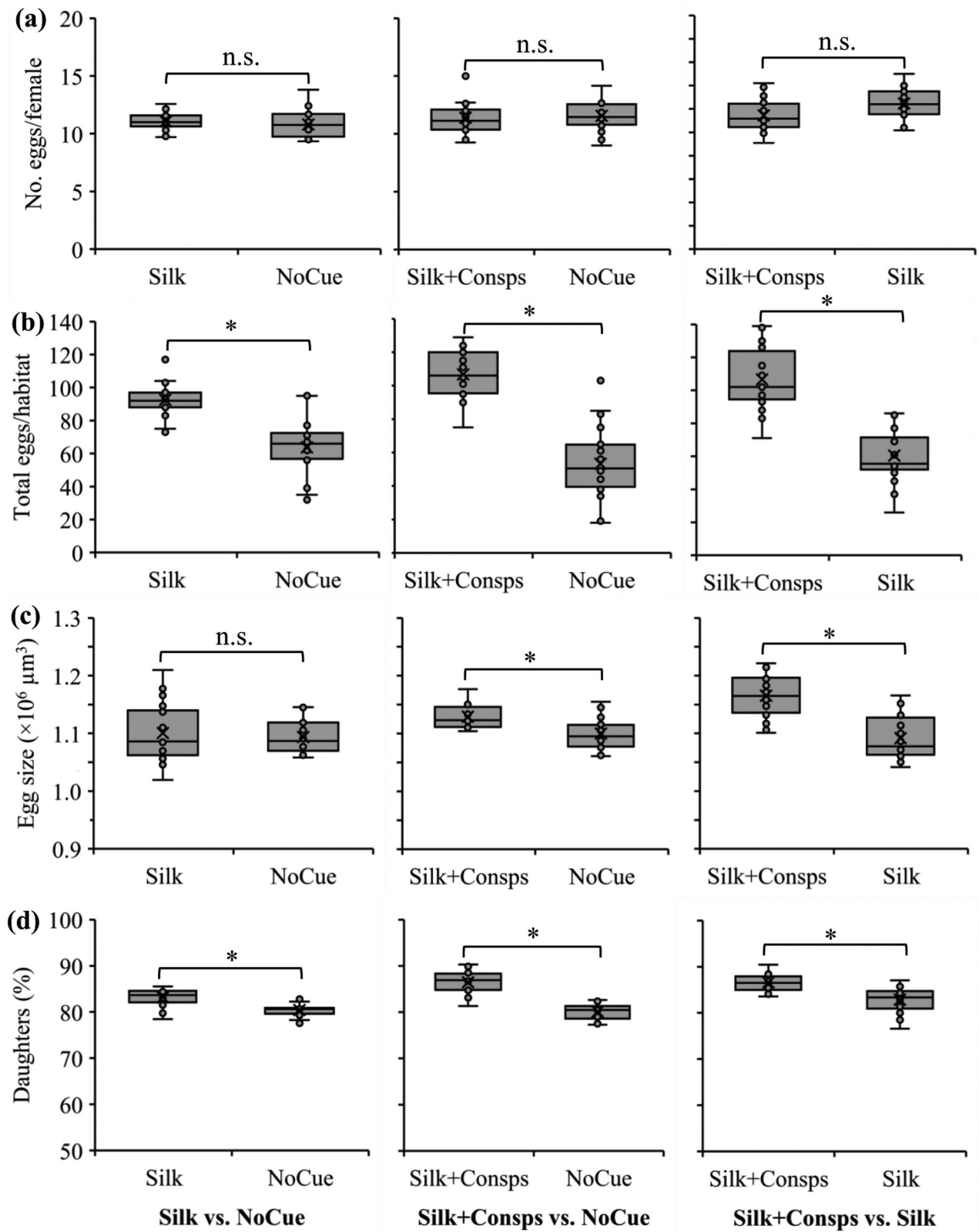
Figure 3. Effects of presence of conspecific cues on number of eggs laid per dispersed female (A), total number of eggs (B), egg size (C), and proportion of daughters (D) in selected habitats in *Tetranychus ludeni*. n.s. indicates non-significant difference ($P > 0.05$), and * indicates significant difference ($P < 0.05$).

settings (Figure 2A), they significantly preferred habitats with conspecific cues, either from silk alone or silk along with additional conspecifics in neighboring habitats, for

settlement (Figure 2B). It has long been recognized that in many web-building species, including spider mites, the presence of conspecifics and webs can increase the probability of
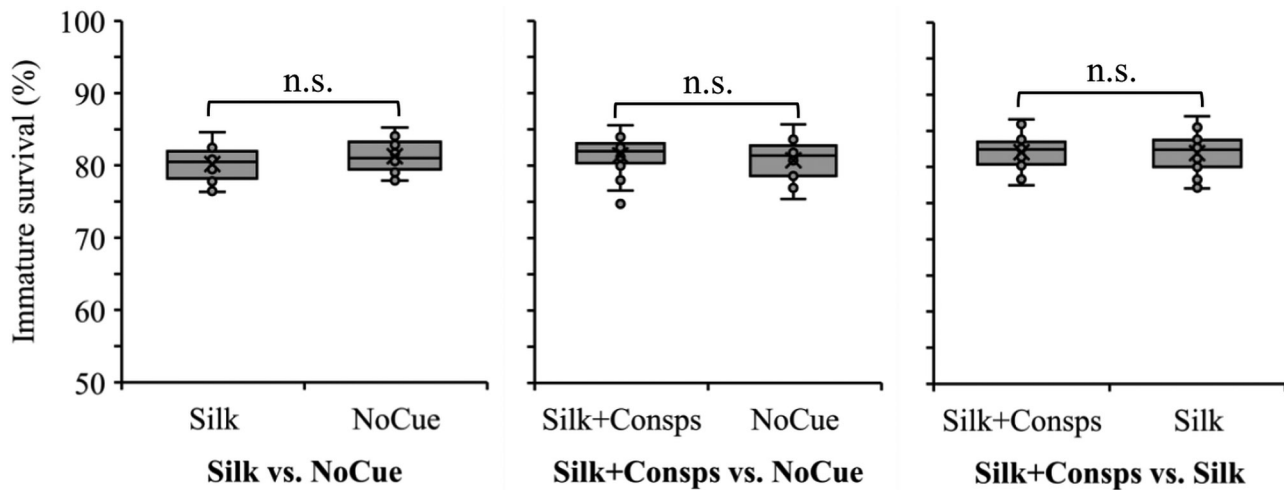
Figure 4. Effects of presence of conspecific cues on immature survival in *Tetranychus ludeni*. n.s. indicates non-significant difference ($P > 0.05$).

settlement (Enders 1977; Leborgne and Pasquet 1987a, 1987b; Hodge and Storfer-Isser 1997; Schuck-Paim and Alonso 2001; Buxton et al. 2020; Schausberger et al. 2021). We show that when given a choice between Silk and NoCue habitats, *T. ludeni* females were more likely to select the silk-covered habitats (Figure 2B). This aligns with previous observations that cues from silk are sufficient to induce conspecific aggregation in spider mites (Yano 2008; Clotuche 2011, 2012a, 2012b, 2014; Carr and Roe 2016). However, silk may not always be the main cause of aggregation displayed by spider mites (Astudillo Fernandez et al. 2012a), because silk only provides short-term indirect positive feedback including recruitment and arrestment (Van Impe 1985; Le Goff et al. 2010). We further reveal that when provided the Silk + Consps and Silk habitats for choice, females significantly preferred the former for settlement (Figure 2B), suggesting that the presence of conspecific cues from ovipositing females in the neighboring habitat induced an additive effect to that of Silk cue on habitat selection in *T. ludeni*. Previous studies also reveal that the presence of conspecifics predominantly influences spider mite dispersal and settlement (Reed and Dobson 1993; Stamps 1994; Stephens and Sutherland 1999), because of the longer-term direct positive feedback through Allee effects, such as higher reproduction and survival in groups (Van Impe 1985; Le Goff et al. 2010; Astudillo Fernandez et al. 2012a, 2012b).

It is known that producing silk in spider mites involves costs of expenditure in energy, protein, and amino acids (Hazan et al. 1974), thus settling on webs that are previously constructed may allow females to save resources and allocate them to egg production (Oku et al. 2009). In this sense, females are expected to lay more eggs in habitats with the presence of conspecifics and webs (Le Goff et al. 2010). Surprisingly, in this study, the presence of conspecific cues did not elevate female fecundity (Figure 3A). Alternately, we show that due to more females settling in habitats with the presence of conspecific cues (Figure 2B), eggs laid in the preferred habitats were significantly higher (Figure 3B). The results may have 2 implications. First, aggregating females adjust their reproductive strategies by restraining their reproductive output due to the increasing population size and density (Krips et al. 1998; Clotuche 2011; Bitume et al. 2013). Second, aggregating in a large group may also entail costs on foraging and feeding efficiency because of the interference among group members

(Bilde et al. 2007; Estevez et al. 2007; Grove 2012; Wong et al. 2013; Li and Zhang 2021; Tinsley Johnson et al. 2021) which may also restrain female fecundity. Females restraining reproductive output (Figure 3A) in habitats with high egg density (Figure 3B) might reduce future food competition and subsequently ensure offspring survival (Figure 4).

Although conspecific cues did not elevate fecundity (Figure 3A), females aggregated in Silk + Consps habitats significantly increased egg size (Figure 3C) and produced a significantly higher female-biased offspring sex ratio in response to the presence of conspecific cues (Figure 3A). These results indicate that *T. ludeni* females facultatively manipulated offspring sex allocation by adjusting egg size in response to the conspecific cues. Previous studies on spider mites have demonstrated that mated females are more likely to fertilize larger eggs that develop into daughters (Macke et al. 2011, 2012; Weerawansha et al. 2022) and produce a higher female-biased sex ratio in the larger and denser populations (Weerawansha et al. 2023). Producing more daughters by the females that aggregate in clusters may decrease resource competition with their offspring because daughters usually mate at emergence and then disperse from the dense environmental conditions (Brandenburg and Kennedy 1982; Boykin and Campbell 1984; Margolies and Kennedy 1985; Li and Margolies 1993; Yano 2004; Osakabe et al. 2008; Clotuche et al. 2013a). Moreover, a female-biased sex ratio of offspring may minimize the local mate competition between sons (Macke et al. 2012; Weerawansha et al. 2023) when females aggregate in habitats with conspecific cues.

Additionally, our results reveal that when provided a choice between Silk and NoCue habitats, the size of eggs laid by females was similar (Figure 3C), but the proportion of daughters was significantly higher in the Silk habitat than that in the NoCue one (Figure 3D). These results suggest that Silk alone did not allow the aggregating females to allocate more nutrients to produce larger eggs; however, ovipositing females may be capable of adjusting the sex allocation strategy to fertilize more eggs in the silk-covered and crowded habitat by lowering the fertilization threshold, above which eggs are fertilized. However, it is noted that the colony of *T. ludeni* was derived from a field population, which might include both *Wolbachia*-infected and -uninfected females. How *Tetranychus* females adjust sex allocation in response to *Wolbachia* infection under various social environments warrants future investigations.

Overall, the study reveals that the habitat choice of *T. ludeni* females is also influenced by the presence of conspecifics. However, conspecific cues from ovipositing conspecifics do not boost female fecundity, although they induce the production of larger eggs that give rise to more daughters. Restraining fecundity while producing more daughters could be the strategy to minimize resource competition and interference among individuals. We also find that ovipositing conspecifics impose an additive effect on Silk cue for habitat selection by *T. ludeni* females. Females tend to settle on silk-covered habitats over those with NoCue; although they lay a similar number of eggs with similar sizes in both habitats, but produce more daughters, suggesting that *T. ludeni* females can adjust the size threshold for fertilization above which eggs are fertilized. Knowledge of this study enhances our understanding in the dispersal and reproductive strategies of spider mites in response to the social environments.

Acknowledgements

Authors' Contributions

N.W., X.Z.H., and Q.W. conceived and designed the study; N.W. collected the data. All authors contributed to data analysis and manuscript preparation.

Conflict of Interest

The authors declare they have no conflict of interest.

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